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THE VELIGER

Concholepas Lamarck, 1801 (Neogastropoda: Muricoidea): A Neogene Genus Native to South America

by

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Abstract. New discoveries of *Concholepas kieneri* Hupé, 1854, in Upper Miocene and Pliocene strata, and *C. nodosa* Möricke, 1896, in upper Pliocene strata of the Pisco Basin (south-central Peru), and *C. concholepas* (Bruguière, 1789) in lower Pleistocene beds of the Talara Basin (northernmost Peru) represent significant temporal and/or geographic range extensions of known species of the genus *Concholepas* Lamarck, 1801. A new middle Miocene species from the Pisco Basin, *C.* ***unguis***, resembles some rapanine species. Shell morphology, paleoecology, and evolutionary timing suggest that the suite of South American species constitutes an endemic lineage and that non-South American species assigned to *Concholepas* are not closely related taxa.

INTRODUCTION

The genus *Concholepas* Lamarck, 1801, includes one living species, *Concholepas concholepas* (Bruguière, 1789), found in the cold-water Peruvian and Magellanic Provinces of western South America. Pliocene species of *Concholepas* have been recognized in Chile (Philippi, 1887; Möricke, 1896; Herm, 1969), but no older records of the genus have been reported from South America, nor have any fossil species been found that might suggest a relationship to other muricid taxa. Efforts to relate the heavy-shelled, shallow-water, Recent *Concholepas* from South America to thin-shelled, deep-water, early Neogene *Lippistes* from New Zealand (Beu, 1970) or to equally ancient taxa from France (Rambur, 1862) and Florida (Vokes, 1972) have not been persuasive. The genus has remained an evolutionary and biogeographic enigma.

This paper presents the first account of *Concholepas* from middle and upper Miocene strata of western South America. It includes a description of *C.* ***unguis*** sp. nov., a morphologically intermediate form with some characteristics of such modern rapanine taxa as *Vasula* Morch, 1861, and *Dicathais* Iredale, 1936. This paper also documents the Neogene distribution of *Concholepas* in Peru, where pre-Pleistocene occurrences of the genus had been unknown, and describes the northernmost occurrence of *Concholepas* near Cabo Blanco, Peru (4°15′S).

PREVIOUS STUDIES

The genus *Concholepas* has been assigned to the muricid subfamily Thaidinae Jousseaume, 1888, by Cooke (1919), Stuardo (1979), and Kool (1987, 1989), usually on the basis of radular characteristics. More recently, Kool (1993) has assigned *Concholepas* to his redefined Rapaninae Gray, 1853, based on anatomy, radulae, and shell morphology.

The shell of *Concholepas concholepas* is large (typically 80–130 mm long and 60–90 mm wide) and robust, with a broadly elliptical aperture whose breadth and extension beyond the spire reflect a rapid rate of whorl expansion (Mabille, 1886; Carcelles, 1954). When the shell is oriented in life position, the pseudumbilical area forms a nearly vertical wall equal to half the dorso-ventral thickness of the shell. The pseudumbilicus is bordered by an arching, cordate, fasciolar ridge that wraps posteriorly behind a straight or recurved parietal flange.

The exterior of the shell is coarsely sculpted with about 10 primary spiral cords and two to four secondary cords in each of the interspaces. The spiral sculpture is intersected in well-preserved specimens by 30–40 small frilled axial costae on the body whorl. The spire is nearly involute on some specimens. Viewed from the ventral side, the spire's axis is rotated clockwise from the long axis of the body whorl.

Concholepas concholepas has been reliably reported from the Peruvian island of Lobos de Afuera (6°27′S) (Sanchez Romero, 1973) to Cape Horn (Stuardo, 1979). This author has encountered late Holocene specimens on the mainland as far north as Salaverry (8°10′S). Populations also occur on the Juan Fernandez Islands, 600 km west of Chile at about 34°S (Stuardo, 1979).

Accounts of *C. concholepas* collected from Mexico (v. Martens, cited in Dall, 1909) are probably in error, as

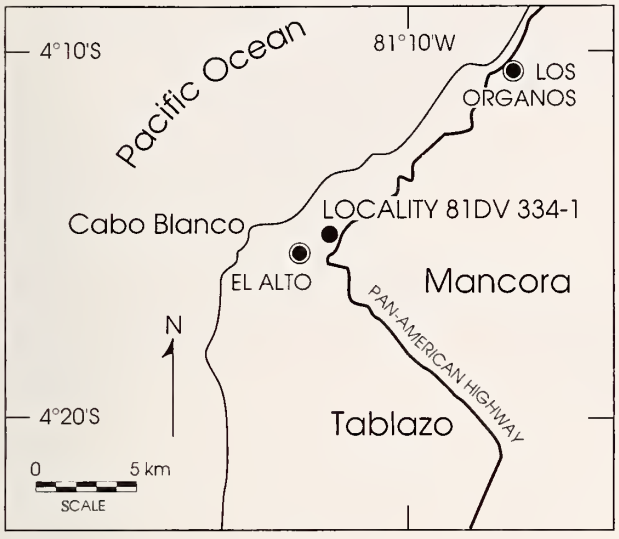


Figure 1

Map showing one locality (81DV 334-1) from which an early to middle Pleistocene specimen of *Concholepas concholepas* was collected near Cabo Blanco, northern Peru. Locality 81DV MT (see text) is from an unknown site on the surface of the Mancora Tablazo.

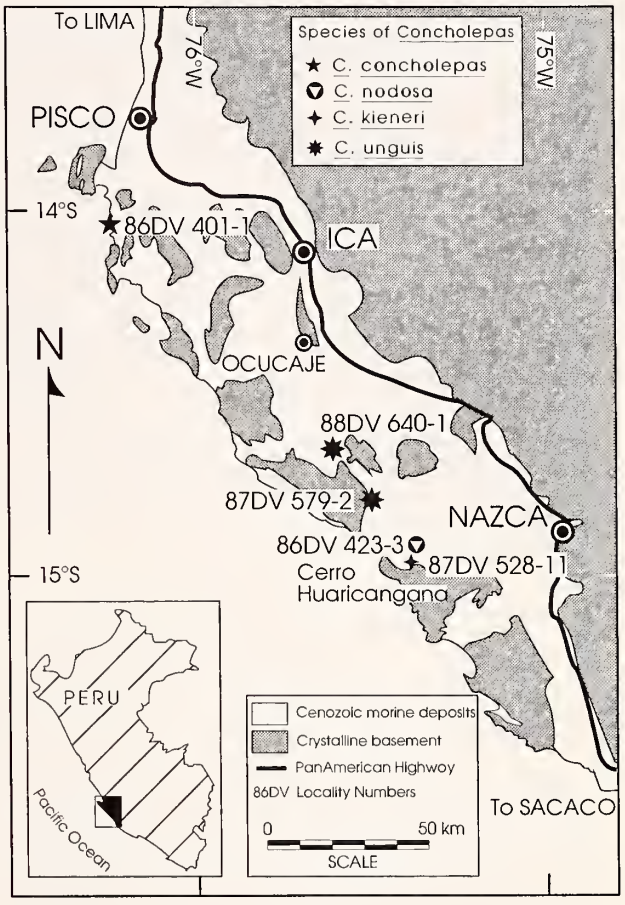


Figure 2

Map of the Pisco Basin, showing outcrops of basement and approximate localities from which specimens of four *Concholepas* species were collected.

are accounts of the species in the Falkland (Malvinas) Islands (Gmelin, 1791), according to Carcelles (1954), who for many years vainly sought examples of *C. concholepas* in the Atlantic Ocean. However, the species has been found in Late Pleistocene middens along the South African coast (Kensley, 1985), demonstrating that populations of this planktotrophic species (Gallardo, 1973, 1979; Castilla & Cancino, 1976) can become established far from the South American mainland.

Concholepas concholepas is known to occur in Pleistocene marine-terrace deposits of Chile (Herm, 1969). Two extinct species, *Concholepas kieneri* Hupé, 1854, and *C. nodosa* Möricke, 1896, have been found in Pliocene deposits along the Chilean coast. The former species is less coarsely sculptured and more fusiform than *C. concholepas,* whereas the latter is more coarsely ornamented with spiral cords, broad smooth interspaces, and axial lamellae. Stuardo's (1979) assignment of an age of 10 million years to *C. kieneri* is based on an outdated definition of the Pliocene/Miocene boundary.

Long before much was known of fossil *Concholepas* in South America, Rambur (1862a, b) described a new middle Miocene species, *C. deshayesi,* from the Loire Basin of France. Tate (1894) described a middle Miocene (not Eocene; see Beu, 1970) species, *C. antiquata,* from Australia. More recently, Beu (1970) reassigned a Miocene New Zealand gastropod, *Lippistes pehuensis* Marwick, 1926, to the genus *Concholepas*. Soon thereafter, Vokes (1972) described a new late early Miocene species, *C. drezi,* from the Chipola Formation of Florida.

GEOLOGY

Fossil and Recent specimens for this study were collected between 1981 and 1988 from the Talara Basin of northern Peru (Figure 1) and Pisco Basin and Sacaco Sub-basin of south-central Peru (Figures 2, 3). These are emergent forearc basins lying between the Peru-Chile Trench and the Andean Cordillera (Thornburg & Kulm, 1981). Post-Eocene bioclastic, shelf and marine-terrace sediments of the Talara Basin have been described by DeVries (1986, 1988). The stratigraphy of diatomaceous and tuffaceous sediments in the Pisco Basin has been detailed by Marocco & de Muizon (1988), Macharé et al. (1988), and Dunbar et al. (1990). The geology and paleontology of the Sacaco Sub-basin is discussed by de Muizon & DeVries (1985).

Geological data presented here were developed by this author unless noted otherwise. Ages based on the diatom zonation of Barron (1985) were provided by J. Barron (see also Macharé & Fourtanier (1987)) and H. Schrader (University of Bergen, Norway), using samples of marine diatoms collected from the Pisco Basin and Sacaco Basin

by Schrader, J. Macharé, and this author. ^{39}Ar-^{40}Ar radiometric ages were provided by L. Snee (U.S. Geological Survey, Boulder, Colorado). Other age determinations are based on a comparison of Peruvian molluscan assemblages with molluscan faunas of Chile (Philippi, 1887; Herm, 1969; Tavera, 1979).

Abbreviations used for localities or specimens are as follows: USNM: Department of Paleobiology, United States National Museum, Washington, D.C., USA; OSU: Orton Museum, Ohio State University, Columbus, Ohio, USA; L: Anterior-posterior Length; W: Width at widest point, perpendicular to length; THK: Dorso-ventral thickness, measured at widest point.

Material is described with a collections number, locality number, and dimensions (L, W, THK). Measurements enclosed by parentheses indicate sizes for broken specimens. Locality descriptions are given in the appendix.

SYSTEMATIC PALEONTOLOGY

Family Muricidae Rafinesque, 1815

Subfamily Rapaninae Gray, 1853

Genus *Concholepas* Lamarck, 1801

Concholepas Lamarck, 1801:69.

Type species (monotypy).—*Concholepas peruviana* Lamarck, 1801 (= *Buccinum concholepas* Bruguière, 1789).

Diagnosis: Shell 30–120 mm long, length : width ratio about 1.2:1, moderately thick, ovate with no anterior constriction; spire rotated clockwise relative to axis of body whorl (viewed from ventral side); sutures usually appressed; aperture broad, 80–100% of shell length; inner lip deeply excavated; columella flattened, flattened surface twists into aperture; strong and elongate fasciolar ridge; very short siphonal canal; deep siphonal notch; sculpture of alternating primary and secondary spiral cords.

Concholepas concholepas (Bruguière, 1789) (Figures 4, 6, 8, 9, 11, 19)

Buccinum concholepas Bruguière, 1789, p. 252.
Purpura concholepas d'Orbigny, 1841, v. 5, p. 437–438; v. 9, pl. 61, figs. 5–7.
Concholepas concholepas (Bruguière). Dall, 1909, p. 168, pl. 22, fig. 1; Carcelles & Williamson, 1951, p. 291; Carcelles, 1954, p. 268–271, pl. 4, figs. 1–11 (with synonymy through 1940); Herm, 1969, p. 136–137, pl. 18, figs. 4a, 4b; Beu, 1970, p. 44, pl. 4, figs. 10–12; Dell, 1971, p. 210–211; Vokes, 1972, Text-figure 2; Marincovich, 1973, p. 35, fig. 73; Stuardo, 1979, p. 10–12, pl. 1, figs. 1–8 (with extensive synonymy).
Concholepas peruviana Lamarck, 1801, p. 69.
?*Concholepas concholepas fernandezianus* Stuardo, 1979, p. 35–36, pl. 2, figs. 9–16, pl. 3, figs. 18–24.

Type Locality: Peru.

Material: OSU 37496, 81DV 334-1, L 78.6 mm, W (59.0) mm, THK (32.5) mm; OSU 37497, 81DV MT, L 76.8 mm, W (62.1) mm, THK (37.0) mm; USNM 447091, Lomas Trash, L 125.9 mm, W 96.9 mm, THK 65.1 mm; USNM 447092, Lomas Trash, L 99.1 mm, W 83.8 mm, THK 48.8 mm; USNM 447100, Lomas Trash, L 90.2 mm, W 74.5 mm, THK 41.4 mm; USNM 447101, 86DV 401-1, L 35.8 mm, W 25.9 mm, THK 13.8 mm; USNM 447109, 86DV 381-5, L 51.7 mm, W (38.7 mm), THK 22.1 mm.

Discussion: Two specimens of *C. concholepas* were discovered in 1981/1982 north of Talara, Peru (Figure 1). One specimen, collected from bioclastic sandstones of the Mancora Tablazo (OSU 37497), has a latest Pliocene or earliest Pleistocene age. The second specimen (OSU 37496) was recovered from a coquina at the base of a terrace intermediate in elevation between the Mancora and Talara Tablazos, which suggests an early to middle Pleistocene age (DeVries, 1988). The Talara occurrences constitute the northernmost occurrences of the genus for any epoch.

Variation within living populations of *Concholepas concholepas* (Schwabe, 1959; Lozada et al., 1976) exceeds that existing between fossil and Recent specimens. Late Pliocene/early Pleistocene specimens of *C. concholepas* from northern Peru resemble neither of the Pliocene species.

Occurrence: Uppermost Pliocene to middle Pleistocene (Mancora Tablazo, northern Peru; marine terraces, south-central Peru to Chile). Upper Pleistocene (marine terraces, south-central Peru to Chile). Holocene (Isla Lobos de Afuera (north-central Peru) to Cape Horn; South Africa; Juan Fernandez Islands).

Concholepas kieneri Hupé, 1854 (Figures 5, 10, 12, 13–16, 21, 22, 25)

Concholepas kieneri Hupé, 1854, v. 8, p. 203; Conq., pl. 3, figs. 4, 4a; Philippi, 1887, p. 55, pl. 6, fig. 1; Stuardo, 1979, p. 21, figs. 20, 22, 25; de Muizon & DeVries, 1985, p. 557, pl. 2, fig. e.
Concholepas nodosa Möricke, 1896; Herm, 1969, pl. 18, fig. 3; Stuardo, 1979, figs. 19, 21.

Type Locality: Coquimbo, Chile.

Material: USNM 447086, 83DV 360-23, L 70.1 mm, W 50.3 mm, THK 27.6 mm; USNM 447087, 83DV 362-6, L 61.7 mm, W 41.8 mm, THK 27.8 mm; USNM 447088, 38DV 361-6, L 102.2 mm, W 67.6 mm, THK 38.0 mm; USNM 447089, 83DV 361-6, L (45.8) mm, W 31.9 mm, THK 16.4 mm; USNM 447090, 88DV 528-11, L 69.0 mm, W 44.8 mm, THK 29.7 mm; USNM 447093, 87DV 562-10, L 57.6 mm, W 42.8 mm, THK 22.0 mm; USNM 447094, 83DV 360-1, L (29.4) mm, W 20.5 mm, THK 12.0 mm; USNM 447095, 87DV 562-4, L (42.7) mm, W 29.1 mm, THK 16.8 mm; USNM 447103, 83DV 370-1, L (74) mm, W 68.2 mm, THK (44) mm; USNM 447104, 83DV 370-1, L (65.5) mm, W (52) mm, THK (28) mm; USNM 447105, 83DV 360-23, L 27.6 mm, W 18.4 mm, THK 9.6 mm; USNM 447106, 83DV 361-6, L 49.1 mm,

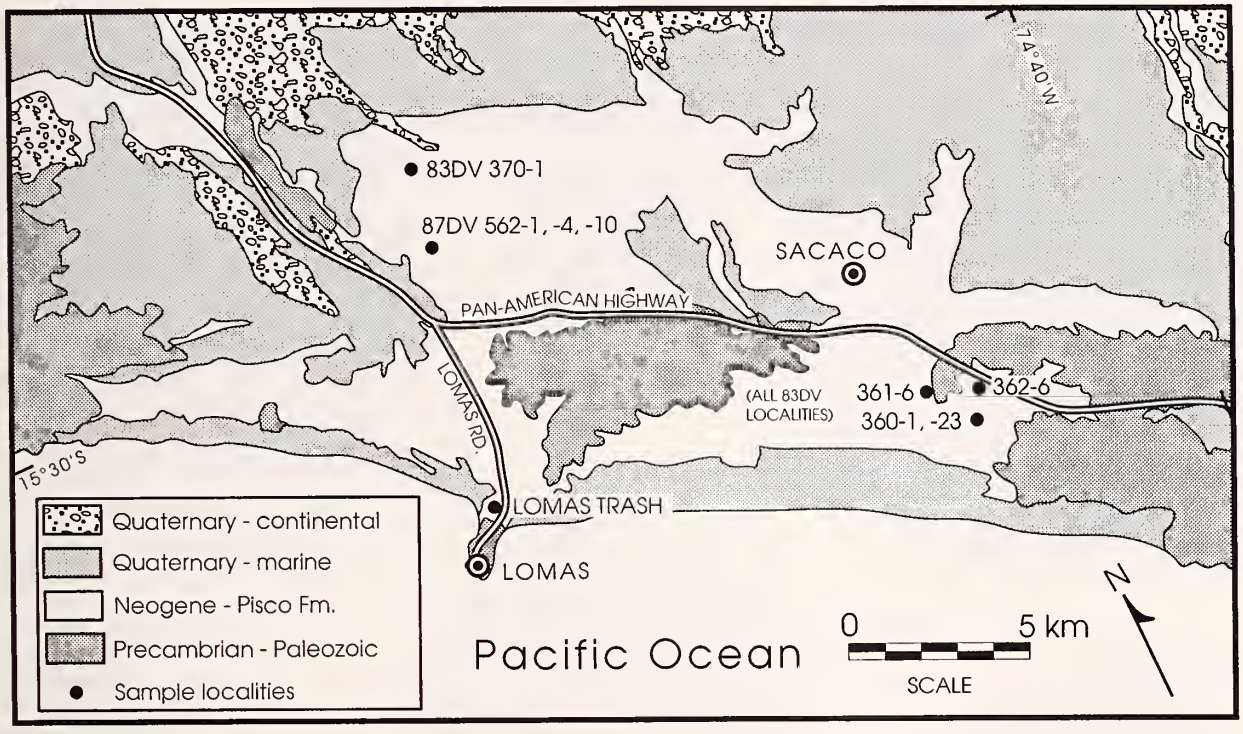


Figure 3

Geological map of the Sacaco Sub-basin, south-central Peru, showing Miocene and Pliocene localities with *Concholepas kieneri*. Geology after de Muizon & DeVries (1985).

W (34.5) mm, THK 15.8 mm; USNM 447107, 83DV 361-6, L (42.7) mm, W 34.5 mm, THK (21.5) mm.

Discussion: Specimens of *C. kieneri* from the Pisco Basin and Sacaco Sub-basin closely resemble specimens from Chile. No consistent differences were noted between Miocene and Pliocene specimens from Peru.

Occurrence: Upper Miocene (Pisco Formation, Peru). Pliocene (Pisco Formation, Peru; La Cueva Formation, Chile).

Concholepas nodosa Möricke, 1896
(Figure 7)

Concholepas sp. Philippi, 1887, p. 55, pl. 58, fig. 12.
Concholepas nodosa Möricke, 1896, p. 560, pl. 11, figs. 14, 15; Herm, 1969, *partim*, p. 137, pl. 18, fig. 1a, 1b, 2.

Type Locality: Coquimbo, Chile.

Material: USNM 447102, 86DV 423-3, L (106) mm, W (81) mm, THK (33) mm; USNM 447110, 86DV 423-3, L (47.7) W (44.8).

Discussion: *Concholepas nodosa* is represented by several specimens collected from a marine terrace that caps upper Miocene and lower Pliocene strata north of Cerro Huaricangana (Figure 2). The terrace deposit contains an unusual fauna composed of extinct Pliocene species and extant Quaternary species, suggesting a late Pliocene/early Pleistocene age.

Stuardo (1979) rightly pointed out the confusion created by Herm (1969), who presented a figure of *C. kieneri* under the name of *C. nodosa,* and by Möricke (1896), who named *C. nodosa* after a juvenile character that is more evident in specimens of *C. kieneri.* Stuardo (1979) further muddied the waters, however, by suggesting that examples of *C. kieneri* with more pronounced nodules on the primary spiral cords (Stuardo, 1979; Figures 19, 21) may be examples of *C. nodosa.*

A comparison of equally small specimens of *C. kieneri* (USNM 447105) and *C. nodosa* (Möricke, 1896: pl. 11, figs. 14, 15) shows that while nodular primary spiral cords occur in both species, the smoother and broader interspaces of the latter species clearly distinguish it from *C. kieneri,* specimens of which have interspaces scored by secondary spiral cords. In larger specimens, such as those figured by Herm (1969), Stuardo (1979), and herein, nodules evolve into coarse lamellae in *C. nodosa* but persist as nodules in *C. kieneri.*

Occurrence: Lower to upper Pliocene (lower and upper Series of Herm (1969) in Chile). Uppermost Pliocene (marine terrace, south-central Peru).

Concholepas ***unguis*** DeVries, sp. nov.

(Figures 17, 18, 20, 23, 24, 26)

Diagnosis: Shell small for the genus with low to moderately elevated spire; fasciolar ridge pronounced; pseudumbilical area narrow, extending only one-third length of shell; surface sculpture of alternating primary and secondary spiral cords of nearly equal strength.

Description: Shell small for the genus, not exceeding 30 mm; ovate, consisting of a broad body whorl (80–95% of the shell length) and usually short spire. Spire consisting of at least two to three whorls; protoconch unknown. Body whorl evenly convex, with no pronounced shoulder and periphery at midpoint of whorl. Anterior quarter of the body whorl faintly constricted; depression behind the fasciolar ridge absent or barely developed; fasciolar ridge strong; pseudumbilical area usually as narrow as fasciolar ridge, extending for less than one-third of shell length. Inner lip excavated, columella slightly thickened and flattened; outer lip moderately thick, with internal crenulations or dentition not visible. Siphonal canal short. Anal sulcus small to non-existent. Surface sculpture consisting of about 13 primary, flattened spiral cords and an equal number of secondary spiral cords, nearly equal in size. Axial sculpture consisting of regular, slightly scalloped and scaly growth lines.

Discussion: The broad, uniformly convex body whorl, long and broad aperture, and strong fasciolar ridge are similar to those of larger specimens of late Miocene *Concholepas kieneri* from the same basin. Moreover, the coiling axis of the body whorl is rotated relative to the axis of the spire in the same clockwise manner as that of more recent species of *Concholepas*.

Specimens of *Concholepas unguis* do not resemble specimens of contemporaneous South American *Acanthina* Fischer von Waldheim, 1807, which have heavier shells and thickened outer lips with a strong labial tooth and associated groove on the body whorl. Specimens of *C. unguis* also differ from Miocene and Pliocene specimens belonging to the muricid genus *Chorus* Gray, 1847, which are distinctly fusiform or pear-shaped and, like specimens of *Acanthina,* have a prominent labial tooth and groove on the body whorl.

No published figures of Chilean mesogastropods resemble *C. unguis* except that of *Fusus sulcatus* (Nobilis in Hupé, 1854). Hupé's specimen shares similar apertural and sculptural traits with *C. unguis* but seems to be more fusiform. The location of Hupé's type specimens is at present unknown (D. Frassinetti, personal communication, August, 1993). No specimens comparable to *C. unguis* were found in collections of the Museo Nacional de Historia Natural (Santiago, Chile) or in collections of J. Tavera at the Universidad de Chile.

The form of *C. unguis*—broad aperture, short spire, excavated inner lip—resembles that of the modern *Vasula melones* (Duclos, 1832), a rapanine species from the eastern Pacific Ocean. In contrast to *V. melones,* the fasciolar ridge of *C. unguis* is more elongate and the coiling axis of the spire is rotated clockwise. Also, larger specimens of *C. unguis* are dorso-ventrally flattened, as in specimens of late Miocene *C. kieneri.*

Type Locality: 14°46′30″S, 75°30′06″W (Lomitas 1:100,000 quadrangle); 2 km NW Fundo Santa Rosa, in hills east of the Rio Ica (Figure 27), about 200 m east of road going to coast, in thin beds of coarse-grained bioclastic sandstone with associated boulders of basement rock (Locality 87DV 579-2). Also found nearby in coarse-grained sandstone horizons within medium-grained and fine-grained tuffaceous sandstone sequences at Cerro Sechuita, east of the Río Ica (Locality 88DV 640-1).

At its type locality, *Concholepas unguis* occurs in an indurated coarse-grained sandstone just above a horizon containing scattered sub-angular boulders of basement rock.

→

Explanation of Figures 4 to 12

Figures 4, 6, 8, 9, 11. *Concholepas concholepas* (Bruguière, 1789).

Figure 4. USNM 447092. Lomas Trash, south-central Peru. Recent. Ventral view showing spire entirely above plane of aperture (×0.75).

Figure 6. USNM 447092. Dorsal view showing rotation of spire relative to body whorl (×0.75).

Figure 8. OSU 37496. Locality 81DV 334-1, terrace between Mancora and Talara Tablazos, northern Peru. Early to middle Pleistocene. Dorsal view. Posterior portion of outer lip is broken, as is spire (×0.95).

Figure 9. USNM 447109. Locality 86DV 381-5, San Juan-Lomas road terrace. Middle Pleistocene. Ventral view. Outer lip broken (×1.00).

Figure 11. OSU 37497. Locality 81DV MT, Mancora Tablazo, northern Peru. Early Pleistocene. Dorsal view, internal sandstone cast (×0.85).

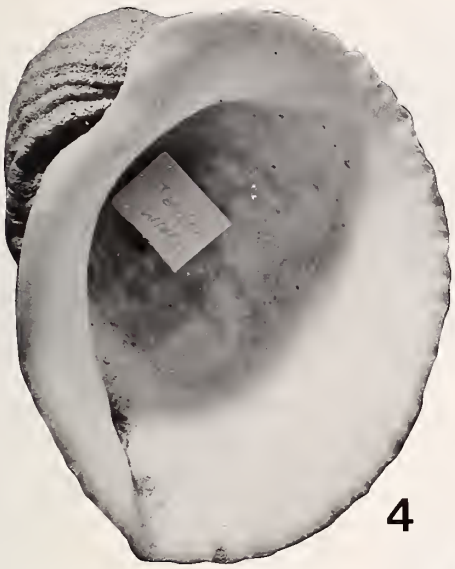
Figures 5, 10, 12. *Concholepas kieneri* Hupé, 1854.

Figure 5. USNM 447094. Locality 86DV 360-1, South Sacaco. Early Pliocene. Ventral view (×1.52).

Figure 10. USNM 447088. Locality 83DV 361-6, South Sacaco. Early Pliocene. Ventral view showing minor encroachment of spire across plane of aperture (×0.75).

Figure 12. USNM 447088. Ventral view (×0.75).

Figure 7. *Concholepas nodosa* Möricke, 1896. USNM 447110, Locality 86DV 423-3, Quebrada Huaricangana. Late Pliocene. Fragment of body whorl and outer lip showing frilled spiral cords and wide interspaces (×0.88).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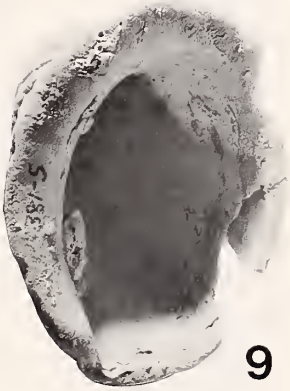
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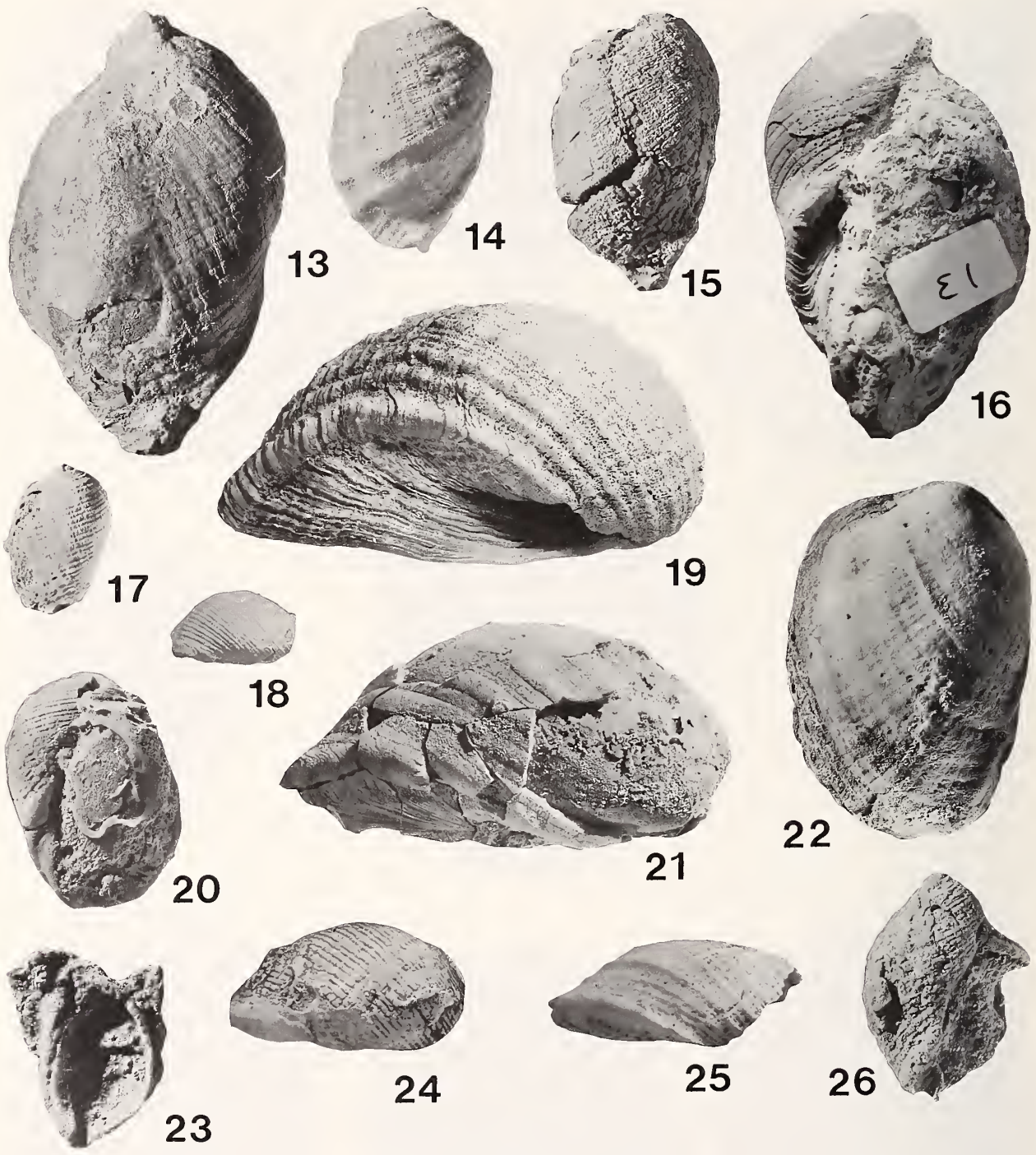

Explanation of Figures 13 to 26

Figures 13–16, 21, 22, 25. *Concholepas kieneri* Hupé, 1854.

Figure 13. USNM 447090. Locality 88DV 528-11, Quebrada Huaricangana, late Miocene/early Pliocene. Dorsal view showing elongate spire. Spire represented by internal cast (×1.03).

Figure 14. USNM 447105. Locality 83DV 360-23, south Sacaco. Early Pliocene. Dorsal view of juvenile specimen showing small nodes on primary cords (×1.42).

Figure 15. USNM 447095. Locality 87DV 562-4, Aguada de Lomas. Late Miocene. Dorsal view (×1.03).

Figure 16. USNM 447090. Ventral view showing atypicaly narrow aperture (×1.03).

Figure 21. USNM 447103. Locality 83DV 370-1, Aguada de Lomas, late Miocene. Lateral view showing modest breadth of pseudumbilical area. Spire represented by internal cast (×1.16).

The boulder bed lies about 30 m above another horizon with basement boulders. The two beds, regarded as disconformities, also occur to the north at Quebrada Gramonal and to the northwest on the west side of the Río Ica (Figure 27). Diatoms collected from tuffaceous siltstones 40 m above the second boulder bed west of the Río Ica yield middle Miocene ages (P. Rønning, 1990, unpublished MS thesis, University of Bergen, Norway), consistent with an ^{39}Ar-^{40}Ar age of 9.22 my for an ash bed slightly higher in the section (Snee, written communication, 1990). Rønning also reports late early Miocene to early late Miocene ages for diatomaceous siltstones between the two boulder beds. Thus, the evidence from west of the Río Ica indicates an early middle Miocene age for *C. unguis* at Locality 87DV 579-2. At locality 89DV 640-1, no microfossils were collected, but the occurrence of *C. unguis*-bearing strata below upper Miocene tuffaceous siltstones and above a regional boulder-strewn unconformity is consistent with a middle Miocene age.

Etymology: "unguis" = nail. The size, shape, and texture of this species recall a thumb and thumbnail.

Material: Holotype USNM 447096, 87DV 579-2, L 25.0 mm, W 19.5 mm, THK 12.3 mm; Paratype USNM 447108, 87DV 579-2, L 15.2 mm, W (10.6) mm, THK 8.2 mm. Referred specimens: USNM 447097, 89DV 640-1, L 20.3 mm, W (12.0) mm; USNM 447098, 89DV 640-1, L (26.2) mm, W (19.6) mm; USNM 447099, 89DV 640-1, L (20.2) mm, W (17.2) mm.

Occurrence: Middle Miocene (Pisco Formation, south-central Peru).

DISCUSSION

Distribution

An understanding of the paleobiogeography and paleoecology of *Concholepas* in South America is hindered by the uneven level of study of Neogene mollusks in South America. Whereas the efforts of Chilean paleontologists have led to a modestly detailed account of Miocene and Pliocene mollusks in central and southern Chile, sporadic research to the north has resulted in a much less complete picture in northern Chile and Peru. Only the molluscan faunas of the Sechura and Talara Basins of northernmost Peru have received as close scrutiny as those of Chile (Olsson, 1932; DeVries, 1986, 1988). Thus, present discoveries of *Concholepas* in south-central Peru fill a significant gap in our knowledge of the genus.

Concholepas unguis has been found only in south-central Peru, in deposits attributable to inner shelf and shallow subtidal environments, based on sedimentological characteristics (ripplemarks, crossbedding, coarse-grained sands) and stratigraphic proximity to boulder-containing disconformities (Locality 87DV 579-2) and basement outcrops (Locality 89DV 640-1). The former locality may be as old as late early Miocene and the latter locality, as young as early late Miocene, but a conservative interpretation of the radiometric and micropaleontological data suggests a probable middle Miocene age. A seeming lack of similarly aged strata in Chile (Tavera, 1979) and limited collecting from Miocene strata in the Sechura Basin of northern Peru (Olsson, 1932) may explain the scarcity of records of early Neogene *Concholepas*.

Discoveries of *Concholepas kieneri* in bioclastic beach deposits adjacent to basement outcrops near Sacaco (de Muizon & DeVries, 1985) extend the range of the species northward by 1500 km. The Sacaco *Concholepas* horizons underlie tuffaceous beds radiometrically dated at 3.9 my (de Muizon & Bellon, 1980; de Muizon & DeVries, 1985) and lie between diatomaceous tuffaceous siltstones dated as early Pliocene (Schrader, written communication, 1986).

Late Miocene occurrences of *C. kieneri* constitute the oldest records of the species in Peru or Chile. Fragments of *C. kieneri,* which are abundant in aprons of bioclastic coquina surrounding former basement stacks near Ocucaje (Figure 2), are between 5 and 7 my old, based on the co-occurrence in laterally contiguous tuffaceous siltstones of the diatoms *Thalassiosira antiqua* and *Rosiella tatsunokuchiensis* (Schrader, written communication, 1986) and ^{39}Ar-^{40}Ar ages of less than 7 my (Snee, written communication, 1990). Late Miocene/Pliocene (*Thalassiosira convexa*

←

Figure 22. USNM 447093. Locality 87DV 562-10, Aguada de Lomas. Late Miocene. Dorsal view (×0.98).

Figure 25. USNM 447105. Lateral view of juvenile specimen. Spire and ventral portion of body whorl broken (×1.48).

Figure 19. *Concholepas concholepas* (Bruguière, 1789). USNM 447092. Lateral view showing fasciolar ridge and broad pseudumbilical area (×.75).

Figures 17, 18, 20, 23, 24, 26. *Concholepas* ***unguis*** DeVries, sp. nov. All middle Miocene.

Figure 17. USNM 447108. Paratype. Locality 87DV 579-2, near Fundo Santa Rosa. Dorsal view (×1.59).

Figure 18. USNM 447108. Lateral view of juvenile specimen (×1.38).

Figure 20. USNM 447096. Holotype. Locality 87DV 579-2, near Fundo Santa Rosa. Ventral view. Aperture mostly obscured (×1.53).

Figure 23. USNM 447097. Locality 640-1, Cerro Sechuita. Ventral view. Spire and dorsum obscured and/or broken (×1.53).

Figure 24. USNM 447096. Lateral view showing short and narrow pseudumbilical area (×1.53).

Figure 26. USNM 447098. Locality 88DV 640-1, Cerro Sechuita. Ventral view. Outer lip and siphonal canal broken (×1.41).

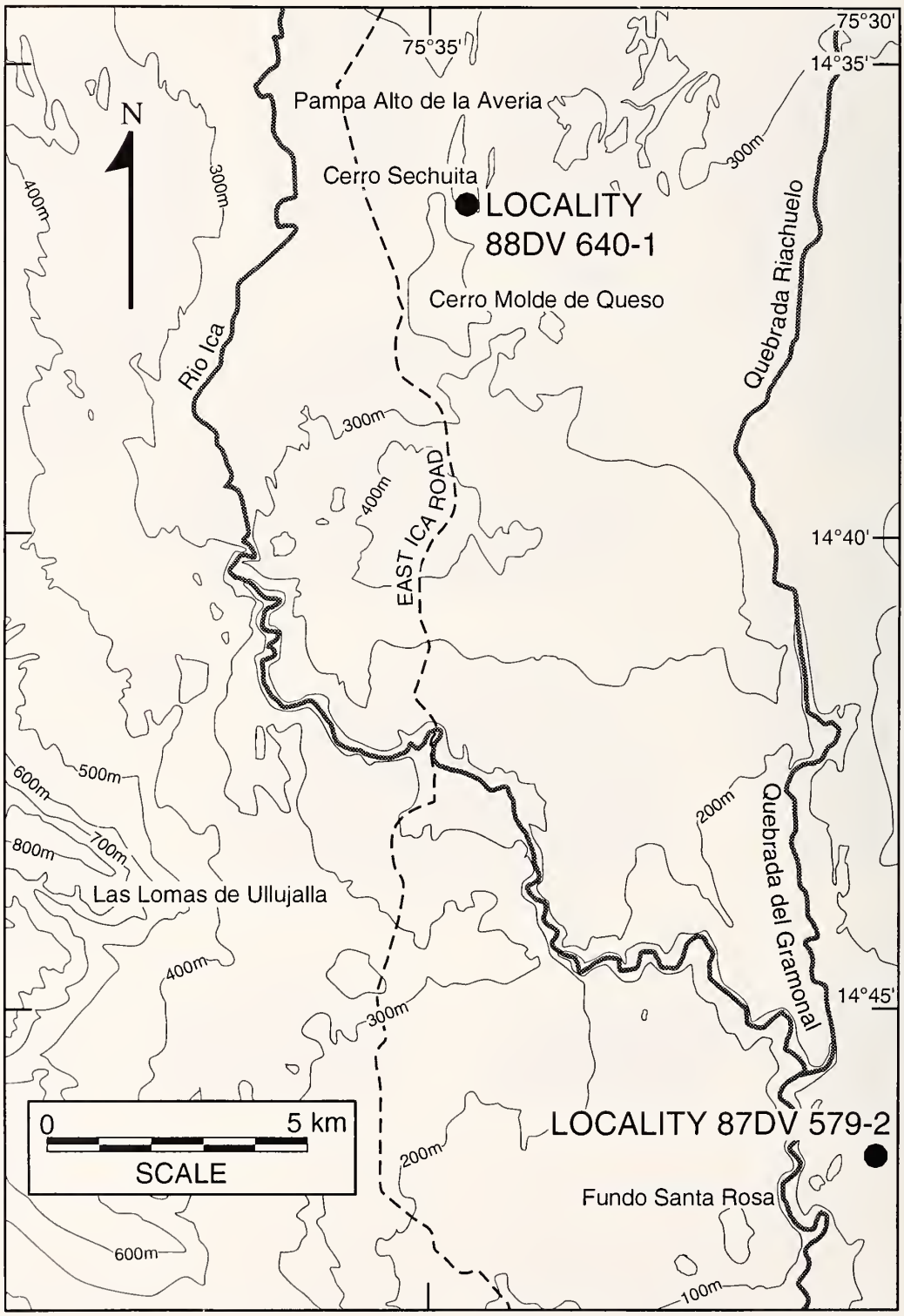

Figure 27

Type locality (87DV 579-2) and a second locality in the Pisco Basin with *Concholepas* ***unguis*** DeVries, sp. nov. Topography and landmarks are adapted from Lomitas 1:100,000 quadrangle map.

"subzone c" and slightly younger, according to H. Schrader, written communication, 1987) specimens of *C. kieneri* also are found in alluvial fanglomerates on the northern wall of Cerro Huaricangana. Specimens from the Sacaco Sub-Basin, at Aguada de Lomas, are found 50–100 m above ash beds dated at 8.8 and 8.0 my (de Muizon & Bellon, 1980; de Muizon & DeVries, 1985).

Specimens of *Concholepas nodosa* occur in a terrace deposit at an elevation of 650 m above sea level on the north side of Quebrada Huaricangana (Figure 2). A late Miocene age for underlying tuffaceous siltstones and mollusks from interbedded sandstone horizons is indicated by microfossils and mollusks. The occurrence of mollusks in the terrace deposit known in the region only since the Pleistocene (DeVries, 1986), together with species previously known only from the Pliocene of Chile (Herm, 1969), suggests a latest Pliocene/earliest Pleistocene age for the terrace fauna.

No examples of *Concholepas* have been reported from upper Miocene beds within the Sechura Basin or in Miocene deposits of the Zapallos Formation of northern Peru, nor have any been discovered in Pliocene beds of the Hornillos Formation of the Sechura Basin. So little effort has been devoted to collecting mollusks from the Sechura Basin (Olsson, 1932; Zuniga y Rivero, 1970; DeVries, 1986), however, that at present little significance can be attached to the late Miocene or Pliocene northern range limit of *Concholepas*.

An examination of Tertiary mollusks in the collections of the Museo Nacional de Historia Natural (Santiago, Chile) and the collections of J. Tavera of the Universidad de Chile in 1993 uncovered no specimens of *Concholepas* from upper Miocene strata of Chile.

Based on what is currently known of the distribution of South American *Concholepas,* it appears that the genus has been represented by a single species (during the Pliocene, two species) within the modern limits of the Peruvian Province from the middle Miocene onwards. *Concholepas concholepas,* which appeared in the intertidal realm at the onset of the Pleistocene Epoch, has shown a great capacity for dispersal in the cooler southern oceans as well as the once-cooler waters of northern Peru (DeVries, 1986).

Evolution

The point at which the fasciolar ridge rises dorsally above the plane of the aperture in specimens of *Concholepas* exhibits a posterior migration progressively from the middle Miocene (*C. unguis*) to late Miocene/Pliocene (*C. kieneri*) to late Pliocene (*C. nodosa*) to Pleistocene (*C. concholepas*). The resulting posterior elongation of the pseudumbilicus in *C. kieneri* was accompanied by dorsal-ventral compression of the body whorl with no anterior constriction. Consequently, the ventral part of the body whorl barely projected downward through the plane of the aperture, allowing more of the aperture's perimeter to press directly against the substrate. Such a configuration might have enabled individuals to better withstand predation or wave impacts on rock surfaces.

The compressed shell of *C. kieneri* seems to have proved weaker as shell size increased after the middle Miocene and as the axial cross-sectional profile became increasingly rectangular in response to the posterior migration of the fasciolar ridge and the modest broadening of the pseudumbilical area. Circumstantial evidence of structural weakness is provided in the illustrations of Stuardo (1979) and by observations of this author, which indicate that shells of *C. kieneri* are more likely to be broken on the dorsal face of the body whorl than are shells of *C. concholepas* or *C. unguis*.

The first adaptation resulting in a stronger shell for *Concholepas* probably was the development of coarse, lamellose, primary cords in specimens of *C. nodosa,* which otherwise remained dorso-ventrally compressed. The inflated body whorl in specimens of *C. concholepas* may have constituted a subsequent and more successful adaptation for strength. Simultaneously, an extreme broadening of a very long pseudumbilical area lifted the newly evolved inflated whorls above the plane of the aperture, thereby retaining a complete seal between aperture and substrate.

Discussions of *Concholepas* evolution have been predicated on the assumption that worldwide, fossil species originally or subsequently assigned to the genus on the basis of ostensibly shared derived characters (flaring aperture, low or submerged spire, and strong fasciolar ridge, according to Beu (1970), Vokes (1972), and Stuardo (1979)) are indeed related. Discoveries in Peru of *C. kieneri* in lower upper Miocene sandstones and a morphologically primitive *Concholepas* species in middle Miocene sandstones require that the evolutionary history of *Concholepas* be re-evaluated. This can be accomplished by examining the morphological and ecological similarities and dissimilarities of South American and non-South American species assigned to *Concholepas* (Table 1).

Shape

Length/width (L/W) ratios of *Concholepas concholepas* average about 1.25; for *C. nodosa* and *C. kieneri,* about 1.40; and for *C. unguis,* about 1.3. All fossil specimens of "*Concholepas*" species found outside of South America have L/W ratios less than or very close to 1.0 (Stuardo, 1979). Two corrections regarding the ratios must be noted. First, the published length and width of the holotype of *Lippistes pehuensis* cited in Beu (1970) are reversed, an error that was perpetuated by Stuardo (1979). Figs. 1 and 3 in Beu's pl. 4 clearly show a L/W ratio of less than 1.0. A L/W ratio measured from the figures (0.804) is the same as one calculated from the published values of height and width, if the values are switched. Secondly, the smaller specimen of "*Concholepas*" *antiquata* figured by Beu (1970; pl. 4, figs. 7–9) has a broken outer lip. With the lip restored,

Table 1

Comparison of shell characteristics of species of *Concholepas* (Lamarck, 1801) and other species previously assigned to *Concholepas*.

Species	L:W ratio	Spire form and position relative to posterior edge of aperture	Body whorl rotation	Sutures	Shell wall thickness	Anterior constriction	Fasciolar ridge	Pseudumbilical area	Posterior notch
Concholepas concholepas	1.25	Submergent, slightly anterior	Moderate	Broadly impressed	Thick	No	Strong	Broad	No
Concholepas nodosa	1.4	Submergent, slightly anterior	Moderate	Broadly impressed	Thick	No	Strong	Mod. wide	No
Concholepas kieneri	1.4	Submergent, even or posterior	Moderate	Appressed	Mod. thick	No	Strong	Narrow	No
Concholepas ***unguis***	1.3	Fusiform, posterior	Slight	Appressed	Mod. thick	No	Strong	Very narrow	No
Lippistes pehuensis	0.8	Submergent, nearly medial	Great	Mod. impressed	Thin	Yes	Weak	Broad	Weak
"*Concholepas*" *deshayesi*	1.06	Submergent, nearly medial	Great	Deeply impressed	Thin	No	Strong	Broad	No
"*Concholepas*" *drezi*	1.1	Slightly emergent and anterior	None	Deeply impressed	Thin	Yes	Strong	Broad	No
"*Concholepas*" *antiquata*	1.0	Submergent and anterior	None	Deeply impressed	Thin	No	Strong	Broad	Strong

the L/W ratio would be much closer to the ratio of 1.0 exhibited by the larger specimen of "*C.*" *antiquata* (pl. 4, figs. 4–6).

Specimens of "*C.*" *drezi* and *Lippistes pehuensis* exhibit an anterior constriction of the body whorl. Specimens of South American species, "*C.*" *antiquata,* and "*C.*" *deshayesi* lack such an anterior constriction.

Spire and Sutures

The spire of *C. unguis* is invariably fusiform, although variably elongate. The spires of *C. kieneri* and *C. nodosa* are usually incipiently submergent or barely emergent, although in rare cases they are markedly fusiform (USNM 447090; Figures 13, 16). Only the spire of *C. concholepas* is typically submergent, but it is with this Quaternary species that non-South American Miocene species (all but "*C.*" *drezi* having submergent spires) are compared.

The spires of all South American species of *Concholepas* are located slightly anterior to, even with, or posterior to the posterior edge of an evenly rounded, non-flaring aperture. The figured holotypes of "*Concholepas*" *deshayesi* and *Lippistes pehuensis* show subdiscoidal coiling with the spires situated nearly medially. The spire of "*C.*" *drezi* is not so centrally located, although it still lies well below the posterior edge of the outer lip, which flares posteriorly and abapically. Only the spire of *L. pehuensis* is located in the same relative position as the spire of South American *Concholepas* species.

The spire in all South American species of *Concholepas* is slightly to moderately rotated in a clockwise direction relative to an axis that joins the siphonal notch with the visible or inferred protoconch. This rotation results from a rapid expansion of the anterior portion of the body whorl. The spires in figured specimens of "*Concholepas*" *antiquata* and "*C.*" *drezi* shows no such rotation, whereas the spires in figured specimens of *L. pehuensis* and "*C.*" *deshayesi* show extreme rotation.

All specimens of *C. unguis,* some of *C. kieneri,* and the spire whorls on specimens of all South American species have appressed sutures. Sutures bordering the body whorls in most specimens of *C. kieneri* and all *C. concholepas* are broadly impressed. In contrast, the spires and body whorls of non-South American species have moderately to deeply impressed sutures.

Fasciolar Ridge and Pseudumbilical Area

The fasciolar ridge in specimens of all South American species of *Concholepas* is well developed, leading to a prominent though short siphonal notch. The pseudumbilical area in specimens of the oldest South American species (*C. unguis, C. kieneri*) is very narrow, whereas in the youngest species (*C. concholepas*), it is unusually wide. *Lippistes pehuensis* has a weak fasciolar ridge, poorly developed siphonal notch, and broad pseudumbilical area. "*C.*" *antiquata,* "*C.*" *drezi,* and "*C.*" *deshayesi* have fasciolar ridges comparable in strength and pseudumbilical areas comparable in size to the Recent South American species, *C. concholepas.*

Paleoecology

Specimens of the oldest known *Concholepas* from South America, *C. unguis,* were found in thin-bedded, coarse-

grained, bioclastic sandstones interbedded with massive, bioturbated, silty sandstones and thick sections of tuffaceous, sandy, diatomaceous siltstones thought to have been deposited close to shore. Similar sedimentological evidence at Aguada de Lomas (de Muizon & DeVries, 1985), where Upper Miocene sandstones contain whole specimens of *C. kieneri,* indicates that for most of the Miocene, *Concholepas* appears to have favored inner shelf, sandy-bottom environments.

Latest Miocene and Pliocene specimens of *Concholepas* in Peru occur together with other epibenthic muricids, trochids, and balanids in aprons of coquina and cobbly alluvium adjacent to former bedrock stacks and coastal promontories. No specimens of *Concholepas* of these ages were found in thin sandstone beds such as those that contain *Concholepas* of middle and earlier late Miocene age.

Late Pliocene specimens of *C. nodosa* and Quaternary specimens of *C. concholepas* are usually found in the bioclastic cobbly sandstones of marine terrace deposits (Herm, 1969). The diversity of rocky-intertidal epibionts and endobionts on *C. concholepas* and on the Peruvian specimens of *C. nodosa* (in contrast to the absence of epibionts and endobionts other than boring algae on specimens of older *Concholepas* species) and the heavier shells of these species suggests that latest Cenozoic populations were adapted to environments subject to higher wave energy than those occupied by their Pliocene or Miocene predecessors.

Middle Miocene Australasian and European species of "*Concholepas*" probably lived at inner to outer shelf depths, judging from the fine-grained sediments in which specimens are found or the molluscan species with which they are associated (Beu, 1970). Specimens of the early Miocene Floridian "*C.*" *drezi* were found close to a contemporaneous coral reef (Vokes, 1972). None of these older thin-shelled species appear equipped to survive in the violent intertidal zone inhabited by *Concholepas concholepas,* the modern species with which the non-South American species are compared.

CONCLUSIONS

New discoveries of four *Concholepas* species in southern and northern Peru establish the genus as a Neogene endemic element of Peruvian-Province molluscan faunas. Evidence suggests that the genus arose from a muricid ancestor during the early or early middle Miocene and with time adapted to progressively higher energy coastal environments. It seems simplest to view the extant species of the South American group, *C. concholepas,* as an example of morphological convergence with an unrelated collection of older deeper-water gastropods from elsewhere in the world. The taxonomic position of non-South American species once assigned to *Concholepas* now needs to be re-evaluated.

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APPENDIX

LOCALITY LIST

81DV 334-1	2km NE El Alto. E end of ridge bounding S side of Army rifle range (no quadrangle maps available). 1-m thick balanid coquina at base of marine terrace intermediate in elevation between Mancora and Talara Tablazo.
81DV MT	Indeterminate locality within the coquinas of the Mancora Tablazo, on plateau between El Alto and Los Organos.
83DV 360-1	15°34′43″S, 74°43′17″W; South Sacaco, NW face of ridge SW of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Bone bed with sandstone concretions at base of ridge.
83DV 360-23	15°34′43″S, 74°43′17″W; South Sacaco, NW face of ridge SW of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Two successive beds of calcareous sandstone and concretionary sandstone

densely packed with valves of the pelecypods *Dosinia* and *Amiantis*.

83DV 361-6 15°34′17″S, 74°43′26″W; South Sacaco, NE rim of depression W of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Mollusk and barnacle beds on upper half of slope, NW of pinnacles of igneous rock.

83DV 362-6 15°34′25″S, 74°43′00″W; South Sacaco, E rim of depression W of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Beds of mollusks at mid-slope below short sandstone ledge by highway.

83DV 370-1 15°27′19″S, 74°49′8″W; Aguada de Lomas, NE corner of depression; N of "Hierro Road" (Llucyuca o Cueva Santa Quandrangle 1:50,000, 1967). Terrace ledge with abundant mollusks in sandstone.

86DV 381-5 15°22′59″S, 75°03′11″W; Ridge at km 47.5 along Lomas-San Juan road (San Juan Quadrangle 1:100,000). Coquina at top of ridge.

86DV 401-1 14°02′31″S, 76°15′51″W; Hueco La Zorra (Punta Grande Quadrangle 1:100,000, 1985), modern beach at north end, just E of first point.

86DV 423-3 14°55′33″S, 75°17′41″W; double-knobbed mesa N of Quebrada Huaricangana (Puerto Caballas Quadrangle 1:50,000). Mollusk bed capping S side of NE knob.

87DV 562-1 15°29′13″S, 74°48′16″W; Aguada de Lomas (Llucyuca o Cueva Santa Quadrangle 1:50,000, 1967). Mollusk beds with *Dosinia* just above cobble bed.

87DV 562-4 15°29′13″S, 74°48′16″W; Aguada de Lomas (Llucyuca o Cueva Santa Quadrangle 1:50,000, 1967). Mollusk beds with *Mulinia* 40 m upsection from 87DV 562-1.

87DV 562-10 15°29′13″S, 74°48′16″W; Aguada de Lomas (Llucyuca o Cueva Santa Quadrangle 1:50,000, 1967). Mollusk beds with *Mulinia* 200 m upsection from 87DV 562-1.

87DV 579-2 14°46′30″S, 75″30′06″W; 1 km E double knob downstream from Quebrada Gramonal, 2 km NE Fundo Santa Rosa (Lomitas Quadrangle 1:100,000). Broken-up area w/ diatomite; platey green siltstone; *Turritella* beds; basement blocks exposed intermittently.

88DV 528-11 14°57′47″S, 75°16′58″W; Third gulch from W, S side Quebrada Huaricangana (Palpa Quadrangle 1:100,000, 1986). Shelly beds at mid-section.

89DV 640-1 14°36′21″S, 75°34′41″W; South end Cerro Sichuita (Lomitas Quadrangle 1:100,000, 1977). Lower flank of hill between two north-south knobs.

Lomas Trash Approximately 15°33′S, 74°50′W; trash heaps of *Concholepas concholepas* on W side of road to Lomas (Yauca Quadrangle 1:100,000, 1982).